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OF

THE LUMBAR ENLARGEMENT

OF THE

SPINAL CORD.

BY

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THE LUMBAR ENLARGEMENT OF THE SPINAL CORD.

I PROPOSE, in the following paper, to notice a few points in regard to the structure of the spinal cord, confining myself chiefly to a description of the course of the fibres forming the nerve-roots, as they pass through the white and gray substances to their final union with nerve-cells, discussing somewhat at length the relation which nerve-cells and fibres sustain in the cord.

In drawing up the descriptive details of this memoir I have restricted them chiefly to the lumbar region in some of the higher vertebrates, lest any deductions I might attempt to establish should be embarrassed by the necessity of comparing observations made upon portions of the cord differing somewhat in structure.

The division commonly made in the substance of the cord into gray and white matter, or into vesicular and fibrous, seems to be tenable only when we state the difference between them to consist in the presence of true nerve-cells in the gray or vesicular, while they are absent in the white or fibrous substance. This distinction seems to me the only correct one, for I am fully satisfied that the so-called *cells of the white substance*, described by Stilling and others, are nothing more than cells belonging to the connective tissue, or, as sometimes occurs, true nerve-cells which have been isolated from the gray substance by the plane of section. Bidder* remarks on the situation of cells evidently connected with the cornua, that "they are sometimes quite encircled by the white substance, in which rare case this substance forms but a very small partition separating them from the gray." This every observer will have noticed, and I have often in longitudinal sections found such cells quite isolated, which I should have considered as belonging to the white substance, had not the section, following a slightly

* Bidder and Kupffer, Untersuch. über die Textur d. Rückenmarks. Leipzig, 1857.

oblique plane, run fully into the cornu lower down. I have never met with true nerve-cells (cells giving off distinct nerve-tubes) in any other situation in the white substance.

My own observations are entirely in agreement with the description which J. L. Clarke* has given of the connective tissue. I have, however, frequently noticed in the cords of adult animals that a few of the cells were still persistent, especially in the vicinity of the posterior cornua, where I have several times seen quite large cells sending out fine processes continuous with the connective tissue. The view which Clarke has taken of the possible relation between connective and true nerve-tissue seems very valuable; for I have long been satisfied of the impossibility of fully distinguishing, with our present means, between these two tissues, which seem to run into each other so closely as to suggest very strongly the important question, "whether there is any actual and essential difference between them, or whether the connective tissue of the cord be intermediate in its nature, passing on the one hand into *nerve* tissue, and on the other into pia mater." † Every observer who has in his possession moderately transparent specimens must be able to satisfy himself of the entire incompleteness of the views of Bidder and others, in whose opinion the greater part of the gray substance consists of connective tissue.

The gray substance is composed of nerve-cells, connective tissue, and nerve-fibres running in various directions, transverse, oblique, and longitudinal.

The form of the gray substance has been so fully and faithfully described and figured by Clarke‡ and Stilling,§ that I shall proceed at once to consider: —

I. *The Nerve-Cells, their Situation, and the Relation which Cells and Fibres bear to each other.*

(A.) *The Nerve-Cells.* — The form of these has been fully figured and described by Clarke, Kölliker, R. Wagner, Stilling, and many others. The cells are subject to great variation, the apparent form, size, and number of processes depending, without doubt, very much on the direction of the plane of section with respect to the situation of the cell. With regard to the distinctions which Jacubowitsch‖ has founded on the size of the cells, dividing them into motor, sensitive, and sympathetic, according to their relative dimensions, I fully agree with Stilling as to the absolute impossibility of making any such classification in our present state of knowledge, and a glance at any of the

* Philos. Trans., 1859, Pt. I. p. 441. † Ibid., p. 442.

‡ Philos. Trans., 1851, 1853, 1859.

§ Neue Untersuchungen über d. Bau d. Rückenmarks. Cassel, 1850 – 59.

‖ Bulletin de l'Académie de St. Petersburg. 1856.

figures which accompany this paper will show cells which, according to Jacubowitsch, should be sensitive, in the anterior cornua, and large or motor cells in the posterior cornua.

The nerve-cell appears to be simply an enlargement of the axis cylinder, containing a granular substance and a nucleus. Sometimes by the use of a power of 700 – 900 diameters I have thought that I detected a cell wall from which the coagulated cell contents seemed shrunken away. With the description which Stilling gives of the minute structure of cell and fibre I cannot at all agree, being convinced, from what little investigation I have been able to make, that the so-called *elementary tubuli* are produced artificially by the coagulating action of chromic acid; and Clarke has recently shown that these appearances may be produced at will in fresh nerve fibre, either by coagulation or mechanical agency.*

(B.) *The Groups of Nerve-Cells, and their Situations.* — The groups of cells situated in the anterior cornua have already been fully described by Clarke, Stilling, and various other authors. I shall confine my own observations entirely to the cells of the posterior cornua, about which greater difference of opinion exists. Bidder and his followers deny the existence of any true nerve-cells in the posterior cornua; in only one case did they observe a large nucleated cell with several processes in the gelatinous substance of the cord of a dog.† Figs. 6, 7 show the relative size and frequency of these cells, and as these two figures are drawn to the same scale as Figs. 4, 5, from the anterior cornua, they will serve for comparison; they are all drawn from the lumbar enlargement of the calf. For convenience of description, I shall adopt Clarke's division of the posterior cornu into *cervix* and *caput cornu*, the *caput* being the broad expanded portion of the cornu, the *cervix* the remainder of the cornu as far forwards as the central canal. My observations on the cells of the posterior cornu, which were mostly made before I had seen Clarke's recent paper (1859),

* Observations on the Structure of Nerve-Fibre. Quart. Jour. of Microscopical Science, January, 1860.

† That other observers have differed from them, Bidder and Kupffer attempt to explain by the somewhat singular hypothesis, that on the one hand cells of connective tissue are liable to be mistaken for nerve-cells, and also preparation by chromic acid "does not preclude the possibility, that, in cutting the section, cells should be torn from their natural situation, and transported to a locality where they do not belong or are not expected to appear." (*Op. cit.*; p. 68.) This latter supposition, even if we could conceive of the possibility "*that, in cutting the section*," cells could be *stolen, and displayed with their processes spread out by the razor*, might be set entirely at rest by making the section from behind forwards, in which case we might certainly infer that all the cells of the posterior portion belonged where they were seen, and the only inference it seems possible to draw is that the preparations of the Dorpat school are not sufficiently transparent for the display of these cells, which certainly require more delicate preparation than is necessary for the cells of the anterior cornua.

are so entirely in agreement with his statements in all important particulars that I shall only notice some of the principal points. The large cells of the gelatinous substance, which Clarke has described as occurring only in the fibrous band constituting the border of the *substantia gelatinosa*, are quite apparent in longitudinal sections, disposed at nearly regular intervals, usually in a single line just above each other, close to the entrance of the posterior roots into the gray substance, seeming to constitute a regular column connected with the posterior roots. With respect to the smallest cells, as well those of the whole posterior cornu as the *substantia gelatinosa*, I have not been able entirely to satisfy myself. Many of the smaller cells belong undoubtedly to the connective tissue, many are merely fragments of larger cells, and it is not improbable that some may be true nerve-cells still in process of development. Fusiform cells* are often met with in the gelatinous substance, and are quite abundant in all parts of the posterior cornu, being frequently found in longitudinal sections. In the central portion of the *caput* the cells are mostly small, though large ones are occasionally seen, and just at the junction between *cervix* and *caput* large cells occur which are sometimes quite thrust out into the white substance, embracing the longitudinal white fibres on all sides with their processes; in some few sections I have met with several cells in this position, forming by their processes quite an intricate network out among the white fibres. In the *cervix* many large cells are met with, together with numbers of smaller size, and here cells are found more or less grouped together, belonging to Clarke's *posterior vesicular columns;* for I cannot agree with Stilling that these cells disappear entirely in the greater part of the lumbar enlargement.†

(C.) *The Relation which Cells and Fibres bear to each other.* — This subject I shall treat under the following heads: — (*a.*) *The Connection of the Nerve-Cells with each other;* (*b.*) *The Connection of the Cells with the Anterior and Posterior Roots;* (*c.*) *The Connection of the Cells with the Longitudinal or White Fibres.*

(*a.*) *The Connection of the Nerve-Cells with each other.* — Schröder van der Kolk‡

* Figured by Clarke, Stilling, and Kölliker.

† Stilling states, in opposition to Clarke, that the posterior vesicular columns, — "(1.) Do not form uninterrupted columns through the entire length of the cord. (2.) They do not enlarge in diameter in the lumbar and cervical enlargements, but disappear entirely in the greater part of these enlargements. (3.) Their greatest diameter is in the dorsal region between these enlargements." In the dorsal region, according to my own observations, they seem to be collected into a compact group, completely circumscribed by a band of fibres, while in the lumbar region they are scattered over a very considerable space, the cells by no means entirely disappearing, however, even in the lower part of the lumbar enlargement. Clarke in his last paper, Philos. Trans. 1859, has somewhat modified his earlier statements.

‡ Bau und Functionen der Medulla Spinalis und Oblongata. Braunschweig, 1859.

describes and figures, for the most part very truthfully, the communications between cells by means of longer or shorter fibres. He states that two cells are often united by more than one fibre, but so far as my own observations reach this is exceedingly rare. He seems to infer that cells of the posterior cornua are also connected, though he does not mention ever having seen this. Lenhossék* speaks of the cells as being multipolar, and connected together in a continuous chain "from the apex of the *conus medullaris* to the inmost structure of the brain"; he figures the union of several cells from the cervical enlargement of the human cord. Bidder and Kupffer† notice the same fact; they were also able to make out cell connections in longitudinal sections. Stilling‡ agrees with the authors cited above, considering these cell connections, however, as independent of those which he believes established between all the cells by the *elementary tubuli.* Both Stilling and Schröder van der Kolk describe the cell-process as bifurcating, distant cells being connected together by this first division, or by means of still further ramification. Stilling carries this division of the cell-process much further than Van der Kolk, making the branches split again and again, till they are reduced to the finest *elementary tubuli.* My own observations agree in this respect much more nearly with the figure and description of Clarke;§ his statement that the cell-processes "divide and subdivide into smaller branches, so that the space between them appears to be occupied by a minute network of the most delicate fibrils," is entirely correct, if we take for granted that Clarke would not carry the splitting so far as to reduce the cell-process to *elementary tubuli*, which appears to be a just inference from his criticisms on Stilling's views.‖ I have uniformly seen the cells connected by fibres *never smaller* than the axis cylinder of the finest nerve-fibres of the white substance, being usually (measured at a sufficient distance from the cell for the diameter to be uniform) about .0001 – .00025″ in diameter.

That *some* cells are connected together by their processes, as described by the authors cited above, admits of no doubt; the results of my own observations, made on the cords of the rabbit, calf, sheep, cat, and ox, admitting of the comparison of many hundred sections, have been very uniform, establishing beyond any doubt connections between *some* cells in every section of average clearness. These connections are by no means so easy to be made out that careful study is not needed to satisfy the observer; a cell-process rarely runs its course on the same plane, so that constant change of focal adjustment is necessary, and the fibres interlace and cross in such confusion, that much

* Neue Untersuch. üb. d. Feineren Bau d. Centralen Nervensystems, (Wien, 1858,) p. 7.

† *Op. cit.*, p. 63.

‡ Neue Untersuch., p. 928.

§ Philos. Trans., 1851, Pl. XXV. Fig. 15.

‖ Quart. Jour. of Microscopical Science, 1860.

patience, and objectives of large angular aperture and very clear definition, ranging in power from 200 to 700 diameters, are constantly needed to satisfy the observer of the truth of what is seen with lower powers. Usually a power of about 120 diameters is best calculated for this study, and with this most of my drawings were made; but sometimes as high a power as 700 is required for the complete resolution of the course of fibres, and none of my drawings were made until the preparation had been carefully studied with high objectives.

Figs. 1, 2, 3, 4, from transverse sections from the anterior cornu, Fig. 5, from a longitudinal section through the same cornu, and Figs. 6 and 7, representing respectively longitudinal and transverse sections from the posterior cornu, may be referred to as exhibiting the different modifications of cell-connection. Sometimes, as at *d*, Fig. 1, the cells are joined by a short, thick fibre; in other cases the process is much longer and usually somewhat thinner (Fig. 1, *c*, and Fig. 2, *d d*); Figs. 3 and 4 give very good examples of both these forms; Fig. 7 shows that these connections are equally met with in the posterior cornua, though they are more difficult to make out here, owing to the finer nature and more complex arrangement of the fibres. Longitudinal sections (Figs. 5 and 6) show chiefly the longer mode of cell-connection; this is especially the case in Fig. 5, from the anterior cornu, where the arrangement of fibres is much easier to make out than in the posterior parts of the cord.

I should, however, state my views very unfairly, did I not urge the great necessity of caution in regard to this question of cell-connection. We are able beyond doubt to see that *some* cells are connected together by their processes, but we are at present by no means able to state, with Lenhossék, that all the cells are connected in a continuous chain; indeed, we have much reason for thinking quite otherwise, the result of a year's observation, principally in this single direction, having convinced me that the undoubted examples of cell-connection, *seen* even in the most favorable specimens, are *exceptional* rather than constant. In a question bearing on all our ideas of nervous conduction so strongly as this does, the necessity for caution in everything like *inference* cannot be too strongly insisted upon.

(*b.*) *The Connection of the Cells with the Anterior and Posterior Roots.* — That fibres of the anterior roots have their origin in cells of the anterior cornu has been fully established by Bidder,* Schilling,† R. Wagner,‡ Stilling,§ and Schröder van der Kolk,‖

* Bidder and Kupffer, Untersuch. über d. Text. d. Rückenmarks, (Leipzig, 1857,) p. 95.

† De Medullæ Spinalis Text. Dorpat, 1852.

‡ Neurolog. Untersuchungen.

§ Neue Untersuchungen.

‖ *Op. cit.*, p. 37.

the only difference between these authors being one of degree; Stilling maintaining that *some* only of the fibres constituting the anterior roots arise from cells within the cord, the remainder being direct continuations of the posterior roots; on the other hand, Bidder and Schröder van der Kolk consider the cells of the anterior cornua the sole origin of the anterior roots. Clarke in his more recent papers acknowledges the cells as a partial source of origin for the roots; he says, "I have seen the processes of the nerve-cells extend so frequently into the anterior roots, that there can be no doubt that some of the latter arise from them."* He also describes and figures this as occurring very frequently in the lumbar and cervical region of the tortoise. That the anterior roots are derived *partly at least* from nerve-cells, is beyond doubt; the principal groups of cells in the anterior cornua are however usually situated at some distance from the border of the gray substance, so that it is often quite difficult to trace these connections; but I have sometimes (though I must admit very rarely) succeeded in tracing, in the cords of small animals, fibres derived from cell processes, not only *into* the bundle of anterior roots, *but quite to their exit from the cord.* This is shown as seen in the cord of the rabbit (Fig. 1, *a'*). Fig. 4 shows a group of cells sending their processes into the anterior roots at *A*; the four cells marked *b* are connected with the bundle of anterior roots by very long, slender processes, and are also connected with each other and with neighboring cells. This is a very interesting group, though, owing to its lying at some distance within the boundary of the cornu, comparatively few of the processes could be traced out into the bundle of roots. Fig. 5 is from a longitudinal section through the anterior cornu; the group of cells is situated quite near the white substance, and a number of cell processes can be traced out into the bundles of fibres forming the anterior roots (Fig. 5, *b*, *b*). Schröder van der Kolk, Bidder, and others, (as stated above,) consider the anterior roots as arising without exception from the cells of the anterior cornua. With this view I cannot agree, for, as it must be acknowledged that at present the fibres we are able to trace with any certainty from cells to the anterior roots are rather the exceptions than the rule, this theory is evidently more the result of inference than of direct observation. On the other hand, we have the fact, the evidence of which I shall discuss further on, that part of the anterior roots are direct continuations of the posterior roots without the intervention in the cord of *any* cells.†

* Philos. Trans., 1859, p. 457; also "J. L. Clarke on the Anatomy of the Spinal Cord," Beale's Archives, 1858, Pt. III. p. 207.

† Schilling maintains that "fibres from the posterior roots never enter the anterior cornu." This is entirely opposed to the observations of Stilling and Clarke, as well as my own.

The connection of the posterior roots with the cells of the posterior cornu has never been determined so satisfactorily; and, as considerable difference of opinion exists among authors, I shall compare somewhat at length the principal views which have been maintained.

R. Wagner* divides the posterior roots into three classes, of which the first pass directly upwards to the brain, without entering the gray substance; the second enter the gray substance and unite with nerve-cells, either collected in groups or strewn singly through the posterior cornua; the third class of fibres, very considerable in number, do not contribute to sensation, but pass to the large cells in the anterior cornua from which the anterior roots arise. Schröder van der Kolk agrees with Wagner, that the true *sensitive* fibres ascend directly to the brain without entering the gray substance, the only fibres from the posterior roots which enter the gray substance being, according to him, the *reflex*, i. e. transverse, and these he infers may enter cells.† Stilling‡ states that he has "never yet succeeded in observing the direct communication of a primitive nerve-fibre of the posterior roots with a nerve-cell of the gray substance, although he maintains this relation between them." Clarke§ describes and figures (Pl. XIX. Fig. 1) cells of the gelatinous substance as continuous by their processes with the posterior roots; of the cells constituting the *posterior vesicular columns* he says, "When the posterior roots of the nerves are traced inwards, they are found to be most intimately connected with all parts of the *posterior vesicular columns*." (p. 445.) He also states, that "the processes of these cells (of the posterior vesicular columns) are prolonged in every direction, — transversely they are continuous on the one hand with the posterior roots of the nerves, and on the other hand with the posterior commissure."‖ These statements are illustrated in the Philosophical Transactions for 1859 by very accurate figures, Pl. XIX. being certainly the *only* correct delineation of the posterior cornu hitherto published. Figs. 6 and 7 of my own drawings illustrate the connections which are seen to exist between cells of the posterior cornu and the nerve roots. In the longitudinal section (Fig. 6), fibres from the cells will be seen to be continuous with the transverse bundles *b*, *b*, and the ascending bundles *c*, *c*, which are direct continuations of the posterior roots, being shown in the figure soon after their passage through the *substantia gelatinosa*, the line *d d* marking very nearly the boundary between the more opaque portion of the *caput* and the *cervix cornu*. Fig. 7, from a transverse section, represents the manner in which the cells are connected with the

* Neurolog. Untersuch., (Göttingen, 1854,) p, 66.

† *Op. cit.*, p. 47.

‡ Neue Untersuch., p. 929.

§ Philos. Trans., Pt. I., 1859.

‖ J. L. Clarke on the Anatomy of the Spinal Cord, Beale's Archives, No. III.

posterior roots, and with various bundles of fibres traversing the posterior cornu in all directions. In transverse sections made from the lumbar region, one or more large cells are usually met with just at the junction between *cervix* and *caput*, on the inner margin of the cornu, these cells being connected with the posterior roots in a manner entirely at variance with all our present ideas of nervous conduction. One such cell is drawn (Fig. 7, *B*), and it will be noticed that, instead of being connected with a *single* bundle, it is connected by its processes with no less than *four distinct bundles belonging to the posterior roots.** It is, moreover, highly probable that these four bundles proceed from different, if not distinct, parts of the body, so that *possibly we have here sensations from four more or less distinct parts of the body, centralized in one nerve-cell;* how they are separately conveyed to the sensorium as distinct sensations I have been able to form no idea, but the fact is extremely interesting. I have been able to satisfy myself from the examination of many specimens that this is by no means an exceptional case, and I think hardly any preparation will be found, at least from the lumbar enlargement, which will not show one or more such cells in this part of the cornu. I have since noticed that Clarke has figured one such cell, occurring in the same part of the cornu, in the cervical enlargement.† In the anterior cornu the same thing is sometimes met with; I have several times seen cells connected with two or more fibres going to different bundles of anterior roots, as has already been figured by Clarke‡ and Schröder van der Kolk.§ It is not easy to observe this in the cords of the larger animals, since the cells from which the anterior roots arise are mostly situated at some distance from the entrance of the roots; but in the smaller animals, as the cat and rabbit, and in the human cord, such cells may often be found; on the contrary, posterior cells of this kind are most easily seen in large cords. The only class of cells belonging to the posterior cornu between which and the posterior roots I have failed to trace any connection, are most of the very small cells met with in every part of the cornu, the nature of which, as stated above, I consider very doubtful. Many of the cells situated in the set of fibres surrounding the posterior cornu may be seen sending out their processes into the posterior roots; this is especially apparent in longitudinal sections, where they are situated one above another at pretty regular intervals, obviously connected with the posterior roots.

* The cells drawn in Fig. 7 are the posterior cells of the *posterior vesicular column.*

† Philos. Trans. 1859, Pl. XIX. Fig. 1.

‡ Philos. Trans. 1859, Fig. 12.

§ *Op. cit.*, Fig. 6.

From what has gone before, it appears that there are probably, as regards origin, the three following classes of nerve-roots, viz.: —

1st. { (*a*) Anterior roots which arise from or terminate in anterior cells.
(*b*) Posterior roots " " " " " posterior cells.

2d. Anterior and posterior roots which meet in cells in the central part of the cord.

3d. " " " " which are directly continuous, i. e. unconnected with any cells in the cord.

The first class consists of nerve-roots which are united, if at all, through the medium of deeper lying cell-groups, those of the last two classes being more directly continuous. I am, however, very far from intending to imply any supposed difference of function between these classes, for I am very strongly convinced that the *function* of cell and fibre is everywhere the same; and one of the principal objects I have had in view in the above classification has been to show how closely anterior and posterior roots are connected, and how nearly they come to having a common origin.

(*c.*) *The Connection of the Cells with the Longitudinal White Fibres.* — This connection can be very plainly made out in the anterior and antero-lateral columns, between cells situated just at the outer margin of the anterior cornu and the adjacent longitudinal white fibres, these latter being seen to be direct continuations of cell processes, passing in a transverse direction a greater or less distance before turning upwards. This course is represented in Fig. 5, *a*, *a*; the bundles formed by these ascending fibres are seen at *a'*. Schröder van der Kolk gives an accurate figure of this derivation of the white fibres (*op. cit.*, Fig. 5), agreeing with Bidder that *all* the longitudinal fibres of the anterior and lateral columns arise from cells. Stilling, on the other hand, maintains "that the whole white substance of the spinal cord (like the separate columns) has a double origin, peripheral and central."

The whole subject of the constitution and origin of the white columns needs careful investigation, more so, perhaps, than any other part of the cord; my own observations have led me to the following views, which are, however, merely an outline of the subject. The anterior and lateral columns, apart from the anterior roots, are only *partially* derived from the cells of the anterior and posterior cornua, *some* of the white longitudinal fibres seeming to be direct continuations of the posterior roots, after these have passed through the gray substance; the posterior white columns are composed almost exclusively of the posterior roots, a few fibres appearing to be derived from cell processes coming from the large cells, situated on the margin of the posterior cornu; what course these latter fibres take after leaving the gray substance I have been unable to determine definitely.

II. *The Course of the Nerve-Roots.*

The course taken by the nerve-roots, both anterior and posterior, as seen in transverse sections, has been described with so much exactness by Clarke, that I shall draw almost all the details of my description from longitudinal sections, which have been less carefully studied.

The Posterior Roots. — These are attached *solely to the posterior columns*, of which they form by far the greater part; this view is in accordance with Clarke (Philos. Trans. 1851), and still maintained in his more recent papers. Stilling, however, regards the lateral columns as receiving some fibres directly from the posterior roots; but after careful examination I am convinced that the fibres Stilling figures in this situation (which I have had no difficulty at all in seeing very distinctly in preparations made by Clarke's method) do not belong to the posterior roots, which from their direction they obviously could not join, but are probably radiating fibres, about to turn upwards into the longitudinal columns; this is especially evident in the cord of the cat, where the sulcus is quite deep, and the bundles constituting the posterior roots are kept very distinct.

Fig. 8, which is an accurate drawing, made by means of the camera lucida, from a longitudinal section across the lumbar enlargement of the calf, will serve to show that the course of the posterior roots within the posterior white columns is exceedingly intricate. The fibres may, however, be seen to take four principal courses: — 1st. Fibres which ascend obliquely upwards and inwards, penetrating sooner or later into the gray substance, according to the degree of their obliquity. (Fig. 8, *b*, *b*.) 2d. Fibres which may be slightly oblique at starting, but soon assume a directly transverse course, sometimes varying this by slightly ascending or descending; these fibres are mostly of the finest sort. (Fig. 8, *e*, *e*.) 3d. Fibres which enter the posterior column at various angles, but very soon bend round, often at quite a sharp angle, descending in a course more or less oblique. (Fig. 8, *c*, *c*.) 4th. Fibres which are looped or recurrent, seeming to unite both ascending and descending fibres. (Fig. 8, *d*, *d*.) Besides these four classes, the first three of which have been already noticed by Stilling, every variety of intermediate course will be found, the bundles of fibres being braided together in the most complex manner.

The fibres of the first class, or *oblique ascending* fibres, seem to be the most numerous, comprising fully one half of the posterior nerve-roots; they usually enter the posterior columns at an angle not far from 45°, pursuing the same course for a considerable distance; after penetrating the outer two thirds of the column, they often vary

more or less from this angle, sometimes curving round and taking a direction nearly transverse before entering the cornu, or, as is sometimes the case, one or two of the fibres enter some one of the cells situated just at the border of the gelatinous substance; usually, however, these bundles curve still more upwards, assuming finally a direction nearly longitudinal, in which case it becomes extremely difficult to follow them; for although they can often be traced a very considerable distance, and are occasionally seen to enter the gray substance, more frequently they are hidden by bundles which cross them, or terminate suddenly, being cut across by the section. It is therefore quite impossible to say with absolute certainty whether *all* these fibres enter the gray substance, or whether part of them are continued upwards to the brain. Many of them may be traced directly into the gray substance, and most of the others converge very gradually, but steadily, towards the same destination, so that, if any fibres continue their longitudinal course upwards to the brain, the number must be very small, by no means sufficient to conduct all the sensitive impressions, as Schröder van der Kolk has imagined. When we examine the *descending oblique* bundles, we shall see that some of these pursue an equally longitudinal course; but surely every one would admit that these must enter the gray substance, rather than be prolonged down into the *filum terminale.* It is therefore highly probable on theoretical ground, and our observations point strongly in the same direction, that *all* the ascending fibres enter the gray substance; still it is to be remembered that this is not yet *anatomically* proved, if indeed it ever can be. This conclusion is also fully in accordance with the physiological experiments of Brown-Sequard * and Schiff,† proving that all the sensitive fibres enter the gray substance within a distance of a few centimeters at most from their starting-point. Intermixed with the oblique ascending fibres may be noticed a variety of bundles, which, instead of pursuing an oblique course, become nearly longitudinal very soon after their entrance into the column, often following a wavy course, interlacing in a very curious manner with the transverse and oblique bundles (Fig. 8, *f*, *f*), doubtless serving to convey sensitive impressions to portions of the cord situated at quite a distance above the entrance of the root. These bundles may *sometimes* be followed through a gradually converging course into the cornu.

The fibres of the second class, or *transverse* fibres (Fig. 8, *e*, *e*), vary but little from this direction; they usually enter the cord as part of some other bundle, depending upon it somewhat for their after course, ascending or descending slightly according to their derivation from ascending or descending bundles. They are sometimes connected

* Comptes Rendus de la Soc. de Biologie, 1855. Journal de la Physiologie, Jan. 1858.

† Lehrbuch d. Physiologie, 1858, p. 250.

with cells just at the margin of the cornu, but usually enter deeply into the gray substance, continuing, as will be shown later, in a more or less transverse course. These fibres appear to be much finer than those of the other classes, and it is therefore difficult to estimate their numerical proportion; they are certainly less numerous than those of the first class.

The fibres of the third class, or *oblique descending*, are quite numerous (Fig. 8, *c*, *c*); they sometimes enter the cord in company with an ascending bundle, following this for a short distance and then bending round, often at a very sharp angle, pursuing an oblique descending course, the exact counterpart of that followed by the oblique ascending bundles. Sometimes the bundle will be seen to divide (Fig. 8, *c'*), part of the fibres immediately entering the gray substance, while a portion plunge farther downwards, thus entering the gray substance at different depths below the starting-point. That all these fibres finally enter the gray substance hardly admits of doubt, since no one could suppose that fibres were indefinitely prolonged downwards, whatever theory might be assumed regarding the ascending bundles. This is fully in accordance with the experiments of Brown-Sequard,* showing that all the descending fibres enter the gray substance within a distance of about five centimeters from their starting-point. I cannot, however, agree with Brown-Sequard that these are more numerous than the ascending fibres; it is sometimes difficult to say with certainty whether a bundle ascends or descends, but notwithstanding this uncertainty the ascending fibres seem considerably more numerous.†

The fourth class, or *looped recurrent* fibres (Fig. 8, *d*, *d*), seem to unite both ascending and descending bundles. Their course is usually as follows: starting from the ascending end of the bundle, the fibres penetrate the posterior column as far as the margin of the gray substance; here the bundle often divides, part of its fibres passing upwards, whilst a part penetrate the gray substance, pursuing a slightly oblique, ascending course; they frequently proceed upwards for a considerable distance, finally looping round and re-entering the white column, joining some bundle with which they pass out, either the root immediately above their entrance, or, as is often the case, one higher up. In tracing the course of such a looped bundle, it is impossible to say

* Comptes Rendus de la Soc. de Biologie, 1855, p. 79.

† Within the gray substance *most* of the fibres from the posterior roots, after traversing the *substantia gelatinosa*, pursue a descending longitudinal course for some distance, as will be seen when we consider the central course of the nerve-roots, and this may *possibly* be the explanation of Brown-Sequard's experiments and deductions.

whether it is ascending or descending, origin and exit being obviously merely descriptive terms when applied to these fibres. These recurrent bundles have already been mentioned by Clarke,* in describing the oblique fibres. "Many of them," he says, "both singly and in small bundles, may be observed to form loops by returning to the white columns." Clarke also mentions, what I have often observed, that a few of the fibres from the oblique bundles "proceed near the surface both upwards and downwards, and pass out again with the roots above and below them." These are also plainly seen in transverse or obliquely transverse sections. Stilling denies the existence of looped returning fibres, assuming that Clarke had been deceived by confounding ascending with descending fibres (*op. cit.*, p. 1186); this, however, is far from being the case. I have been able repeatedly to verify Clarke's statement, and have frequently been able to trace such bundles or fibres from root to root, both in longitudinal and transverse sections. These looped fibres appear to occur frequently in the nervous system of some of the lower animals, especially in *Lumbricus terrestris*, as described by Clarke † and Faivre, ‡ in the abdominal cord of which they are very numerous.

The above description of the fibres derived from the posterior roots agrees mainly with Stilling's, differing, however, in regard to the fourth class. My reason for not following the classification of Clarke has been, that I felt obliged to arrange the fibres entirely with reference to their course within the posterior white columns, from the conviction that neither of the three central courses according to which Clarke has mainly classified them originated from any one particular set of fibres belonging to the posterior columns.

The Central Course of the Nerve-Roots. — In longitudinal sections made parallel to the median fissure, the *substantia gelatinosa* is seen to be traversed by numerous bundles of fine fibres, running transversely through it, nearly parallel to each other.

The three different classes of fibres mentioned above — viz. ascending, descending, and transverse — pass indiscriminately into these *central* transverse bundles (Fig. 8), which are, as Clarke has already noticed, often somewhat fusiform in appearance. I have uniformly found that these bundles pursue the same central course in the lumbar enlargement which he has described with so much accuracy in the cervical enlargement of the cat; § after traversing the *substantia gelatinosa* in a direction nearly transverse, they curve round, some upwards, some downwards, running a considerable distance as longitudinal fibres, forming by their union those bundles which are seen

* Philos. Trans. 1853, p. 350.

† Proceedings of the Royal Society, Jan. 27, 1857.

‡ Histologie Comparée du Syst. Nerv. Paris, 1857.

§ Philos. Trans. 1853.

cut across in transverse sections, especially well marked near the junction of *cervix* and *caput cornu*. These longitudinal bundles are often of quite considerable size (Fig. 8, *h*, *h*). Clarke states that he has "not seen them distinctly below the cervical enlargement"; they are certainly more strongly marked, in the cat at least, in the cervical region, where they may be seen with very great distinctness, but I have had no difficulty in making them out very clearly in all my preparations from the lumbar enlargement of the calf. Clarke has described these bundles as "running down the cord," and this is usually the case, though occasional variations will be met with, bundles sometimes running upwards (Fig. 8); the great majority of fibres, however, undoubtedly run downwards.

These bundles of longitudinal fibres, which I propose to call *longitudinal columns of the cornua*, send out fibres anteriorly in all directions, many of them becoming connected with large cells which are found grouped along the whole length of these columns, belonging to Clarke's *columnæ vesiculares posteriores*. Fig. 6 represents the relation in which the cells stand to the longitudinal columns (*a*, *a*, *a*); they are also seen on a smaller scale in Fig. 8. The fibres composing these columns do not seem to follow a longitudinal course for any considerable distance, but usually soon pass onwards towards the anterior cornu. Many of the fibres pass obliquely to the commissures, both anterior and posterior; some pass out into the lateral white columns, while others pass forwards, becoming connected with cells, or else directly into the anterior roots, with which they are often continuous. Others assume every variety of upward or downward curve before reaching their final destination, a longitudinal section through the anterior cornu often presenting an inextricable web consisting mostly of cut-off fibres (Fig. 8).

A part of the transverse bundles which traverse the *substantia gelatinosa* do not seem to be connected at all with the *longitudinal columns of the cornua*, their fibres being plainly seen to cross these at right angles; they are mostly continued anteriorly for a very considerable distance, often becoming lost to view (or cut off), but may sometimes be seen to be directly continuous with the anterior roots.

It will be noticed in my description of the course taken by the fibres derived from the posterior roots, that I have given but little attention to that part of their course which is mainly traceable in transverse sections; this there was no need of doing, since Clarke has described it with *so much accuracy* in his latest paper (1859). I have myself verified most of the results at which he has arrived, and can add nothing.

Clarke states in his description of the longitudinal columns of the cornua, that a part of their fibres "form loops with each other within the gray substance, particu-

larly near its border; others extend directly into the anterior white columns, and bending round, both *upwards* and *downwards*, are seen sometimes to re-enter the gray substance and form with each other a series of loops, and sometimes to continue a longitudinal course within the anterior white columns, amongst the fibres of which they become lost. Whether the latter also ultimately form broader loops with corresponding fibres from the gray substance, it is impossible to ascertain. But even if those which *ascend* in the anterior columns are continued upwards to the brain, one can scarcely avoid inferring that those which *descend* re-enter the gray substance, either to form loops or to become continuous with the fibres of the anterior roots, since the whole of the latter, as we shall presently see, proceed directly from the gray substance."* This formation of loops near the border of the anterior cornu I have often noticed, and while I have no doubt that some of these loops found in the anterior columns are derived from the posterior roots, as stated by Clarke, I am convinced that a large portion of the looped fibres which are found in great abundance in the inner portion of the anterior white columns have a different origin, viz. from the cells of the anterior cornua, to which I have in some cases succeeded in tracing one or both ends of such fibres.†

The Anterior Columns and Roots. — The anterior white columns contain the following elements: — (1.) The anterior roots which traverse them in a slightly curved ascending course; and (2.) Fibres which vary from longitudinal to every variety of curved course, often forming loops which may be traced a greater or less distance through the column. These loops are formed in the following manner: bundles of fibres, some of which arise from cells near the margin of the anterior cornu (Fig. 8, *l*, *l*), may be traced in a longitudinal section, descending obliquely until they emerge from the gray substance into the anterior white column; here they continue the same general direction, finally curving round (as seen at *k*, *k*) and re-entering the gray substance; in my description I have traced this bundle downwards, — it is obviously impossible to say whether the fibres ascend or descend.

Fibres belonging to these bundles may sometimes be seen to join cells at both ends

* Philos. Trans. 1853, p. 349.

† Stilling entirely denies the existence of looped fibres anywhere, with the singular criticism, that "Clarke would allow that he had not followed the fibres in question continuously from the nerve-root on, through white and gray substance, into the white columns, and from these back again into the gray substance." (*Op. cit.*, p. 1186.) This is the more extraordinary, since Clarke not only states that these fibres are *seen* to form such loops, but also figures them. (Philos. Trans. 1853.) It is by no means a very difficult thing to follow fibres quite across the cord in the smaller animals, such as the cat, from which Clarke's figure is drawn.

of the loop, thus standing probably in mediate connection with the anterior roots. Occasionally these fibres accompany the anterior roots for some distance, in which case they appear to share the origin of the anterior roots, either arising from cells or being direct continuations of the posterior roots, bending round subsequently, and pursuing either an ascending or descending course, finally curving round to re-enter the gray substance. A few of the curving fibres found in the anterior columns pass out a short distance with some bundle of anterior roots, leaving this soon, and curving upwards or downwards to join some other bundle of roots, either above or below, with which they pass out from the cord.

In concluding this paper, I cannot but feel fully aware of its extreme incompleteness; it expresses, however, the constant work of a year, during which time I have had occasion continually to feel grateful for aid and encouragement from kind friends, in which connection I cannot fail to mention the constant interest and kindness of Dr. O. W. Holmes, and my great indebtedness for many useful suggestions to Professor Jeffries Wyman, without whose aid I should hardly have begun this work, and certainly should not have carried it through.

The accompanying figures have all been drawn by myself, by means of the camera lucida; and although much interesting detail is necessarily omitted, I have endeavored to make them faithful representations of the most important facts, my constant effort having been to give too little detail rather than too much. I have etched them on copper myself, believing that microscopic drawings are too apt to lose much of their truth even in the hands of the most careful artist, and that a faithful, though somewhat rough transcript of the original drawing, made by the observer himself, must be of greater value than a more highly finished copy.

Conclusions.

1. That true nerve-cells exist only in the gray substance, these cells being connected by their processes in more or less definite groups; but not probably, as some authors maintain, so as to form an uninterrupted chain from brain to *filum terminale.*

2. That the anterior roots arise partly from nerve-cells, another portion being directly continuous with the posterior roots. A part of the posterior roots also enter cells.

3. The roots may therefore be divided into three classes; — such a division does not, however, imply any functional difference.

(1.) Anterior and posterior roots which arise from or terminate in anterior or posterior cells.

(2.) Anterior and posterior roots which meet in cells near the central part of the gray substance.

(3.) Anterior and posterior roots which are directly continuous.

4. That bundles of anterior roots are connected with those above and below, by looped fibres proceeding from cells which some of the roots enter; these fibres leaving the gray substance, and passing sometimes upwards, sometimes downwards through the anterior columns, finally curving inwards to join some other bundle of anterior roots with which they pass into the gray substance.

5. That thus fibres from nerve-cells after passing upwards through the longitudinal white columns, do not *all* continue onwards to the brain, but most of them re-enter the gray substance at a greater or less distance from the point of exit, sometimes probably becoming again connected with cells, and again emerging from these as longitudinal fibres.

6. That the processes from a single nerve-cell, whether in the anterior or posterior cornu, do not necessarily *all* pass into the *same* bundle of roots, but often pass into three or four different bundles; a cell process also sometimes sending branches into different bundles. Thus we may have sensitive impressions from different parts of the surface conveyed to one cell, and motor impulses distributed from one cell to different points.

7. That all the anterior and probably all the posterior roots enter the gray substance, though the posterior roots often pass into the cornu at a considerable distance from their first entrance into the cord.

8. That most of the fibres from the posterior roots, after traversing the posterior columns, are collected into transverse bundles, traversing the *substantia gelatinosa* in a slightly ascending course; after passing through which they curve downwards (*sometimes* upwards), forming, by the longitudinal course which they then maintain for some distance, a very interesting series of longitudinal bundles, which I have called *longitudinal columns of the cornua*, standing in very close relation to the *posterior vesicular columns* of Clarke, with the cell processes of which many of their fibres are continuous.

9. That some of the bundles which traverse the *substantia gelatinosa* do not pass into the *longitudinal columns of the cornua*, but proceed directly across the gray substance, becoming continuous with the anterior roots.

10. That the posterior white columns are composed almost entirely of the posterior roots, which merely traverse them before entering the gray substance. They appear, however, to receive a few fibres from cells situated on the extreme margin of the posterior cornua, and some more or less longitudinal fibres from the looped recurrent bundles.

11. That the posterior roots are connected by curved fibres or bundles of fibres, proceeding from one root and curving round after penetrating the gray substance, becoming connected with some other root above or below. The same is seen in transverse sections with regard to roots situated side by side, both anterior and posterior, the looping fibres sometimes proceeding directly from root to root, and sometimes passing through cells.

From which it results that the same fibre must in different parts of its course conduct both centrifugally and centripetally.

12. That, besides the looped recurrent fibres, the three principal courses taken by the posterior roots before entering the gray substance are with reference to a longitudinal plane, ascending oblique, descending oblique and transverse.

The method of preparation usually employed was a modification of Gerlach's and Clarke's, although many others were employed, according to the object in view. The following method gave the best results from which to make drawings. Thin sections from the cord, hardened in alcohol, were washed a few minutes in pure water, and then immersed in glycerine, to which Gerlach's solution of carmine,* previously filtered, had been added; in this the sections were allowed to remain four to eight hours, according to the tint desired (a light tint interfering least with the details and sharpness of outline). I have been able to obtain more delicately colored specimens and more clearly defined structure by the use of glycerine than by any other method. The sections are then washed first in pure water, afterwards with strong alcohol, in which they are allowed to remain about an hour, and are now ready for preparation with turpentine, according to Clarke's method; they may be put up in Canada balsam, or, as I have found very advantageous, in thick, colorless copal-varnish, which often preserves minute details better than balsam. Although Stilling and others have found much fault with Clarke's method of preparation, on account of the too great transparency it sometimes gives, I am convinced that, with practice and some slight modifications, it is the only one suited to the minute study of the cord, other methods seeming to me, after thorough trial, quite unsatisfactory as compared with Clarke's. As a hardening material, I have often employed chromic acid with considerable advantage; but when coloring-matter is used, alcohol is most suitable, and is certainly much easier to succeed with.

* Gerlach, Mikroskopische Studien, Erlangen, 1858. Solution of carmine in water, to which a few drops of strong ammonia have been added.

Explanation of the Plates.

Fig. 1. Transverse section representing part of the anterior cornu, from the lumbar enlargement of the rabbit. *a*, *a*, *a'*, bundles of fibres belonging to the anterior roots; in the bundle marked *a'* two cell processes can be traced to the outer boundary of the cord; *b*, *b*, outer boundary of the white substance; *c*, *c*, boundary of gray substance; *d*, *d*, cell connectives of the short, thick variety; *e*, a longer cell connective. Drawn by the camera lucida, with one of Nachet's microscopes, from a preparation magnified 160 diameters; the scale is in hundredths of a millimetre.

Fig. 2. Group of cells from the anterior cornu of the sheep, connected with the radiating bundles from which the longitudinal fibres of the white substance are derived. *a*, *a*, *a*, radiating bundles; *B*, a large cell, sending its processes, *b*, *b*, *b*, into four different bundles; *c*, a process passing forward towards the anterior roots; *d*, *d*, long cell connectives. Figs. 2 to 7, inclusive, were drawn by the camera lucida, with eyepiece No. 1, objective $\frac{4}{10}$ of one of Smith and Beck's first-class instruments, giving a power of 120 diameters; the scales affixed express thousandths of an inch. *This and the following figures are all from the lumbar enlargement.*

Fig. 3. Group of cells from the anterior cornu of the sheep, connected with the anterior roots at *A*; *B*, fibres radiating to the side of the cornu; *C*, fibres passing to the interior of the cornu. This figure represents a somewhat deeply lying group of cells as seen in a transverse section.

Fig. 4. Group of cells connected with the anterior roots, as seen in a transverse section, from the anterior cornu of the sheep. *A*, entrance of the anterior roots into the cornu; *b*, *b*, *b*, *b*, cells connected by long, slender processes with the anterior roots; *c*, *c*, boundary of the cornu. In this figure almost every variety of cell connection may be seen, with bundles of fibres crossing in every direction.

Fig. 5. Group of cells connected with the anterior roots, from a longitudinal section through the anterior cornu of the sheep. *A*, white substance; *B*, gray substance; *a*, *a*, cell processes passing upwards to form the ascending fibres of the white substance; *a'*, *a'*, bundles of ascending fibres; *b*, *b*, cell processes passing into the anterior roots; *b'*, *b'*, anterior root bundles; *c*, *c*, descending fibres and bundles (*c'*). Different forms of cell anastomosis may also be observed in this figure.

Fig. 6. Longitudinal section through the posterior cornu of the calf, drawn just inside the gelatinous substance, on a plane with the entrance of the posterior roots. *a*, *a*, *a*, ascending bundles of fibres, *longitudinal columns of the cornua*, connected on the one side with the posterior roots, and on the other with cells which belong to the *pos-*

terior vesicular columns; *b*, *b*, transverse bundles of fibres; *c*, *c*, ascending oblique bundles, seen in many places passing into the longitudinal bundles; *d*, *d*, line marking the boundary between *cervix* and *caput cornu*, the figure comprising chiefly the *cervix*.

Fig. 7. Transverse section through part of the posterior cornu of the calf, showing the side of the cornu next the median fissure with the entrance of the posterior roots. The figure gives part of the *caput cornu* immediately adjoining the gelatinous substance, with most of the *cervix;* a line drawn parallel to the bottom of the paper, through *B*, would about mark the junction between *cervix* and *caput;* *a*, *a*, boundary of the cornu; *a'*, *a'*, bundles formed by the posterior roots; *B*, a large cell, sending four of its processes into four different bundles of posterior roots.

Fig. 8. Longitudinal section completely through the lumbar region of the cord, from the calf, the section which is parallel with the median fissure comprising both anterior and posterior columns and roots. *A*, anterior white columns; *P*, posterior white columns; the intermediate space representing the gray substance; *a*, *a*, *a*, anterior roots; *k*, *k*, looping fibres connecting two different bundles of anterior roots; *l*, *l*, descending bundles within the gray substance, which seem to be the origin of the fibres, *k*, *k*; *m*, *m*, descending fibres; *n*, *n*, ascending fibres; *c*, *c*, descending oblique fibres in the posterior columns; *b*, *b*, ascending oblique fibres; *e*, *e*, transverse fibres; *c'*, descending bundle, part of which enters the gray substance, another portion continuing a descending course within the white column; *d*, *d*, looped fibres, forming loops within the gray substance (several examples of this are seen along the boundary between gray and white substances); *f*, *f*, bundles which continue in a longitudinal course for a considerable distance; *p*, *p*, bundles of posterior roots outside the cord; *g*, *g*, transverse bundles of fibres traversing the *substantia gelatinosa;* *h*, *h*, *longitudinal columns of the cornua* formed from the transverse bundles *g*, *g;* *s*, bundles which are cut across by the plane of section (many such will be seen in various parts of the gray substance); the cells are merely sketched, the magnifying power being too low to give any detail of their connections with the fibres. This figure was drawn by the camera lucida with eye-piece No. 1, objective $1\frac{1}{2}$ inch, giving a power of about thirty diameters. The scale is in hundredths of an inch.


Fig. 1.
mm.
Fig 2
Fig. 3.
A.
B.
C.

Fig. 4.

A.

120 ×

Fig. 5.

B.

A.

120 ×

001"

Fig. 6.

Fig. 7.

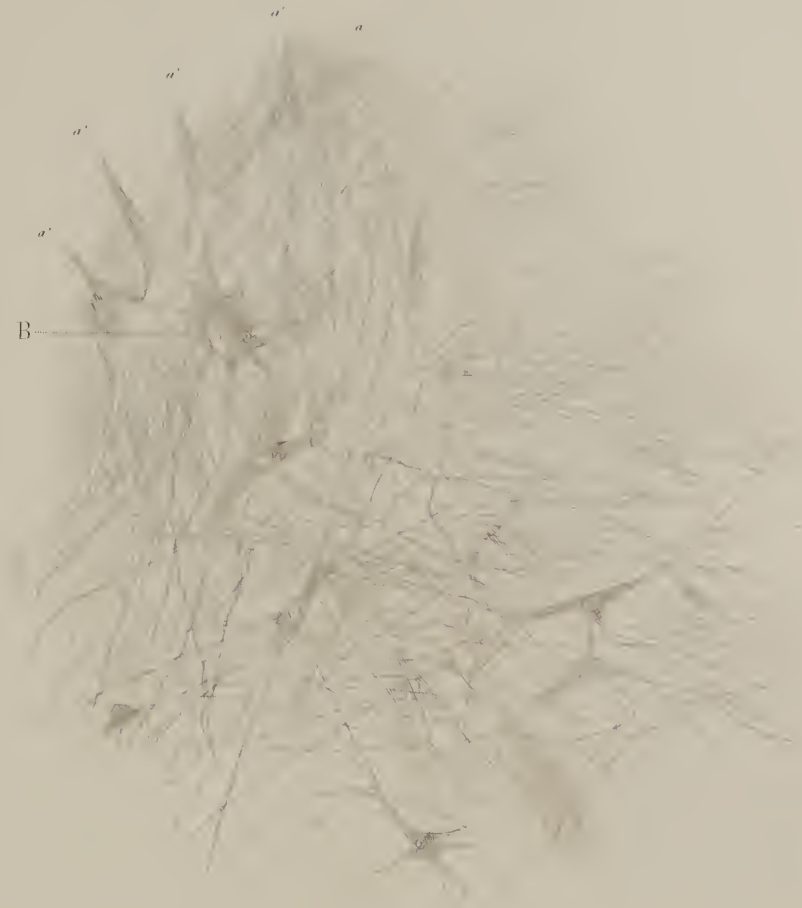

Fig. 8